THE BRYOZOAN GENUS *SKYLONIA* THOMAS (CHEILOSTOMATA)

BY

A. J. KEIJ

c/o Shell Internationale Petroleum Maatschappij B.V., The Hague, Netherlands

Pp. 215–233; 4 *Plates*, 3 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 24 No. 3
LONDON: 1973

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 24, *No.* 3 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 9 *August* 1973 *Price* £1.30

THE BRYOZOAN GENUS *SKYLONIA* THOMAS (CHEILOSTOMATA)

By A. J. KEIJ*

CONTENTS

		Page
I	Introduction and Acknowledgements	217
II	Systematic Affinities of *Skylonia*	218
III	Environment	220
IV	Distribution	220
V	Systematic descriptions	224
VI	References	232

SYNOPSIS

The anascan genus *Skylonia* Thomas is monographed, comprising six species of which four new species and two subspecies are erected here, ranging from the Middle Eocene to Late Miocene, possibly Pliocene. First known from the Eocene of Cuba and Mexico, *Skylonia* achieved a circumtropical distribution by Miocene times.

I. INTRODUCTION AND ACKNOWLEDGEMENTS

The genus *Skylonia* was introduced by Thomas in December 1961 for a problematical fossil, *Skylonia mirabilis*, found in the Lower Miocene of Kenya. Thomas compared *Skylonia* with the Bryozoa but rejected its affinities with this group. Almost simultaneously Sandberg (1962) introduced the genus *Fusicanna* for a Miocene species, *Fusicanna dohmi*, of the Dominican Republic and placed this genus in the bryozoan family Fusicellariidae (Cheilostomata, Ascophora).

The author's interest in the genus *Skylonia* was aroused, for while employed as a palaeontologist for Brunei Shell Petroleum Co., in northwestern Borneo, he had found these peculiar spindles in the Tertiary sediments of Sarawak and Sabah (Malaysian Borneo) and Cebu (Philippines), prior to the publication of the papers by Thomas and Sandberg. In 1962 and 1963 all the East Asian material was presented to the British Museum (Natural History) in London to enable Dr H. D. Thomas to prepare a monograph on the genus. Meanwhile additional material of a related, but apparently undescribed, genus had been found by Dr Y. Nagappa in the Eocene of Assam and by Dr R. Lagaaij in the Eocene of Belgium and of Libya together with *Skylonia* species from the Eocene of Cuba and the Neogene of Nicaragua and Indonesia. Dr D. A. J. Batjes supplied some Miocene specimens from Trinidad, Dr R. J. Scolaro from the Lower Miocene of Florida. The present author found some specimens in the Middle Eocene of Mexico and in the Upper Neogene of Fiji. Unfortunately, owing to the untimely death of Dr Thomas, the planned monograph did not materialize. This was the situation when the Trustees of the British Museum kindly allowed the author to study their *Skylonia* collection.

* C/o Shell Internationale Petroleum Maatschappij B.V, The Hague, Netherlands.

During this study valuable additional topotype material of *Skylonia mirabilis* Thomas was received from the British Petroleum Company Ltd and of *Skylonia dohmi* (Sandberg) from Dr P. A. Sandberg.

The larger part of the *Skylonia* material here described has been deposited in the British Museum (Natural History), London (numbers Z 934–956, 978–984 and D 51492–51853, 51855–51869) and the remainder in the Rijksmuseum van Geologie en Mineralogie at Leiden, Netherlands (numbers RGM 172524–172547).

I wish to thank all who contributed material for my study, especially the British Museum (Natural History) in London, the Union Oil Company of California, Dr P. A. Sandberg (Urbana, Illinois, U.S.A.) and Dr W. J. Clarke of the British Petroleum Company Ltd. I am particularly grateful to Dr R. Lagaaij and Miss P. L. Cook, who both critically read and discussed the manuscript. Permission from Shell Internationale Petroleum Maatschappij B.V. to publish this paper is gratefully acknowledged.

II. SYSTEMATIC AFFINITIES OF *SKYLONIA*

The systematic position of *Skylonia* within the Cheilostomata invites some comments. In the controversy between Thomas (1961) and Sandberg (1963) as to whether *Skylonia* is a bryozoan or not, I am inclined to side with the latter. The following characters, in my opinion, support the bryozoan nature of *Skylonia* (see also Sandberg 1963, p. 17). (1) Colonies consist of elongate, erect spindles apparently originally connected to an incrusting, e.g. stolonate, base by a cuticular joint. (2) The camerate structure is bryozoan-like. The chambers are quadrate to hexagonal in outline on the outer surface and they are similar in size to those found in Bryozoa. (3) The chambers are arranged in a number of longitudinal rows around the axis of the spindle. (4) Chambers alternate in adjacent rows. (5) Chambers inter-connect by simple communication-pores. (6) Each chamber has a single aperture on the outer surface of the spindle. (7) Openings interpreted as rootlet pores occur at the proximal and distal extremities of the spindles.

I agree with Sandberg that *Skylonia* belongs to the Cheilostomata. Sandberg, however, placed *Skylonia* in the Ascophora, whereas I am inclined to assign it to the Anasca on account of two additional characters. The first is that spindles of *Skylonia* show at their proximal end, which is often somewhat curved, a single large initial zooecium, the " anascaform zooecium " of Sandberg (1962, p. 65). A similar wide open and slightly tilted initial zooecium occurs in several Upper Cretaceous or Lower Tertiary Anascan species, such as *Encicellaria hofkeri* Keij, *Stamenocella oculata* (Ulrich and Bassler), " *Cellaria* " *mucronata* Meunier & Pergens, and in more complete specimens of the species referred to " *Smittipora* ? " by Labracherie (1968, p. 315). The first species occurs in the Maastrichtian of Maastricht, the second in the Paleocene Vincentown Limesand of New Jersey, the third in the Montian " Calcaire de Mons " in a boring near Mons, Belgium, and the fourth in the Bartonian blue marls of the Falaise de Handia near Biarritz in France. In the first two species there is no evidence of ramification, in the third species at least lateral ramification occurs, and in the fourth species distal ramification only, via chitinous joints, can

be inferred from the paired basal rami at the distal extremity of the internodes. In *Skylonia* there is no evidence of distal jointing.

The second characteristic feature is the frontal closure of the zooecia. A more or less dome-shaped calcareous lamella is developed with a small to fairly large, circular to transversely elongate opening in its centre (*vide* the " blind zooecia " of Canu & Bassler 1920, text-fig. 23). This feature, too, is known only from a number of anascan genera. In some of these genera an arcuate impression is sometimes observed distal to the central opening, corresponding in shape and position to the distal outline of the operculum, and indicating that closure developed just beneath the frontal membrane. Genera with calcareous closures in which such " opercular scars " occur are marked with an (*) in table 1; others, including *Skylonia*, in which they are definitely absent, are marked with a (−). It would seem, therefore, that in these various genera calcareous closures do not always develop in identical fashion.

In *Skylonia* all zooecia in the spindle, with the exception of the initial one, are as a rule closed, although spindles without calcareous closures, presumably representing unaltered opesiae, do occur (Pl. 1, fig. 13; Pl. 2, fig. 2; Pl. 3, fig. 9; Pl. 4, figs. 3, 6 and 7). It appears that the spindles are either entirely with, or devoid of, such calcareous closures, in contrast to the situation found in the Maastrichtian *Encicellaria hofkeri* Keij, where some spindles had their proximal zooecia closed and their distal zooecia still open and probably functioning at the time of death. Closed zooecia are found quite commonly in species of genera belonging to the suborder Anasca, and especially in the division Malacostega. They occur both in incrusting and in articulating, erect, species. A survey made by Dr Lagaaij of illustrations in literature and of his extensive collection produced examples in species belonging to the following genera (table 1).

TABLE 1

Anascan genera in which calcareous closures may occur

Division Malacostega	
Family Membraniporidae	*Biflustra*(−), *Conopeum*(*), *Vincularia*(*)
Cupulariidae	*Cupuladria*(*)
Electridae	*Pyripora*(*)
Hincksinidae	*Ellisina*(?), *Setosellina*(−)
Calloporidae	*Callopora*(?), *Membraniporidra*(?), *Mollia*(−), *Parellissina*(?), *Planicellaria*(*), *Retevirgula*(?), *Stamenocella*(*)
Fusicellariidae	*Fusicellaria*(−), *Encicellaria*(−)
Skyloniidae	*Skylonia*(−)
Division Coilostega	
Family Onychocellidae	*Thyracella*(*)
Microporidae	*Vibracella* (*Discovibracella*)(*)
Division Cellularina	
Family Farciminariidae	*Nellia*(*)
Scrupocellariidae	*Scrupocellaria*(*)

(*): opercular scar observed; (−): opercular scar not observed; (?): unknown.

A few examples of closed zooecia with or without opercular scar are figured here, i.e. *Nellia tenuis* Harmer (Recent, South China Sea—Pl. 1, fig. 7), *Scrupocellaria milneri* Canu & Bassler (Oligocene, Byram type locality, U.S.A.—Pl. 1, fig. 8), *Stamenocella oculata* (Ulrich & Bassler) ? (=*Planicellaria oculata* Ulrich & Bassler 1907, non d'Orbigny 1851) (Paleocene, Vincentown limesand, U.S.A.—Pl. 1, fig. 3), *Planicellaria fenestrata* d'Orbigny (Thanetian, Musitu, Prov. Vitoria, Spain—Pl. 1, fig. 1), *Vincularia fragilis* (Defrance) (Lower Lutetian of Nalinnes, Belgium—Pl. 1, fig. 2). This phenomenon may even have led to the introduction of new species. Two examples are known from the older literature. *Planicellaria fenestrata* d'Orbigny (1851, pp. 37–38) and *P. oculata* d'Orbigny (1851, p. 37) were described by d'Orbigny from the same locality, the Maastrichtian of Néhou (Manche) in NW France. I strongly suspect that *P. oculata* represents specimens of *P. fenestrata* of which the zooecia were closed-off by a calcified lamella leaving only a relatively small opening in the centre. *P. oculata* was designated the type species of the genus. A similar situation is suspected for two Middle Miocene species of *Scrupocellaria* described by Reuss (1848) from the Leitha Kalk of Eisenstadt. *Scrupocellaria schizostomata* (Reuss) (1848, pl. 9, fig. 9) might well represent *S. granulifera* (Reuss) (1848, pl. 9, fig. 6) with the zooecia occluded by calcareous lamellae.

III. ENVIRONMENT

Skylonia is often found in association with larger benthonic Foraminifera such as the Middle Eocene *Polylepidina chiapasensis* Vaughan in Mexico, or *Operculina–Lepidocyclina–Amphistegina* species in the Miocene of Borneo, or *Miogypsina–Lepidocyclina–Taberina* in the Middle Miocene of Kenya. The living larger benthonic Foraminifera, such as the infaunal *Operculina* and the epifaunal *Amphistegina*, *Heterostegina* and *Peneroplis* all carry symbiontic zooxanthellae in their protoplasm and are therefore restricted to the photic zone of shallow, tropical seas.

A characteristic assemblage of other Bryozoa is found together with *Skylonia*, consisting of species of *Nellia*, *Vincularia*, *Margaretta*, *Crisia* and *Poricellaria* (see table 2). These are all cellariiform genera, i.e. having erect, branching, flexible (jointed) colonies, which are attached to their substratum of rock, indurated sediment, plants etc. by rootlets. According to Stach (1936, p. 63) the cellariiform growth form " is adapted for life in the littoral zone ". The kinetic energy of the water must have been moderate, sufficiently high to prevent mud from settling and choking the bottom fauna, but not so high that it detached the bryozoan colonies.

The above evidence suggests that *Skylonia* lived in shallow, tropical to subtropical holomarine seas at depths estimated not to have much exceeded 50 m.

IV. DISTRIBUTION

The oldest known *Skylonia* species occurs in the Middle Eocene of Mexico and Cuba and the Upper Eocene of Cuba (*Skylonia bermudezi* n. sp.) (see text fig. 1). No Oligocene *Skylonia* species are known yet. In the Early Miocene, however, *Skylonia* was established in Borneo with *Skylonia sarawakensis* n. sp. (see text figs. 1 and 2) and *S. sandbergi* n. sp., and in Trinidad, Nicaragua and the Dominican

TABLE 2

Bryozoan assemblages found associated with *Skylonia*

● : dominant
○ : common
\+ : rare

	Middle Eocene—Mexico	Lower Miocene—Nicaragua			Lower Miocene (Sarawak)	Lower Miocene (Sarawak)	Lower Miocene (Sarawak)	Lower Miocene (Sarawak)	Lower Miocene (Sarawak)	Middle Miocene (Sarawak)	Middle Miocene (Sarawak)	Middle Miocene—Madura	Middle Miocene—Kenya	Middle Miocene—Trinidad	Upper Miocene (Sabah)	Upper Miocene (Sabah)	Upper Miocene—Cebu	Upper Miocene/Lower Pliocene—Fiji
		500 m	560 m	640 m	Bu 509	Ca 53	Ca 54	R 860	R 861	J 1065	Mu 823	Be 1421	REC 2082	DB 268	Jo 121	Mt 2196	My 1994	DEV 18
Canda												+						+
Cellaria												+						
Celleporidae			+	+								○		+				
Crisia	○				○	+	○		●			●	+					●
Cyclostomes indet.								+									+	
Gemellipora														+				
Idmonea	○						○											+
Lichenopora												+						
Margaretta		○	○	+	+					○	○	●	+				+	+
Metrarabdotos		●	●	●										+				
Nellia	●	●	●	●	○	●	●	+	+	+		●	●	●				+
Pasythea	●		+									●	○				+	
Poricellaria	+							+				●	+					+
Savignyella												+						
Scrupocellaria			+									+	+	+	+			+
Semihaswellia	○																	
Sertella												●						+
Skylonia	○	+	+	+	+	+	+	+	+	+	+	+	○	+	+	+	+	+
" Smittipora "	○																	
Steganoporella												+						
Thalamoporella	○?		+	+								○		+				+
Tremogasterina				+														
Vibraculina			+															
Vincularia	●				+	+	+				+	●	●		●	+	●	+
Vittaticella	+											●	+	+				+

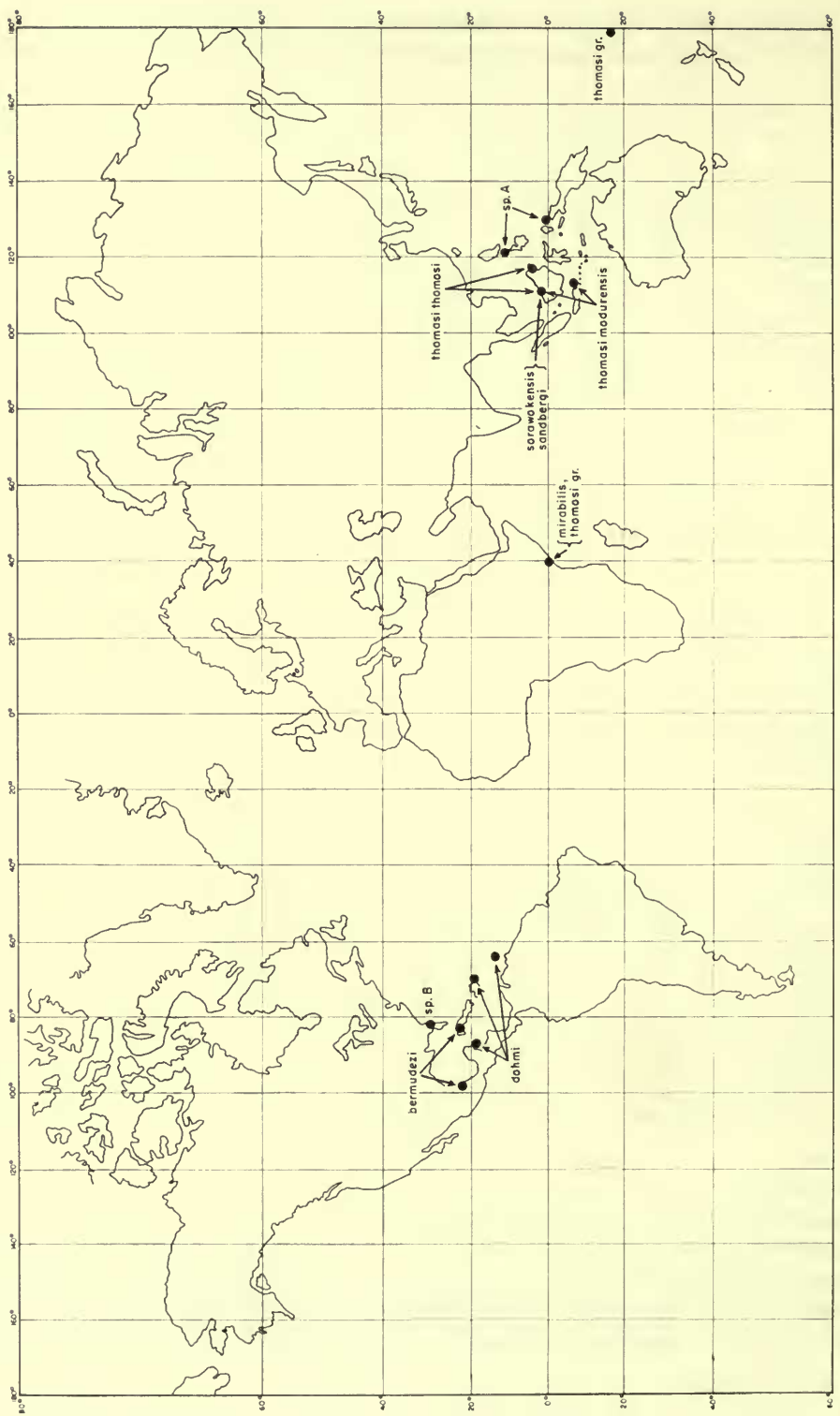


FIG. 1. Distribution of *Skylonia* species.

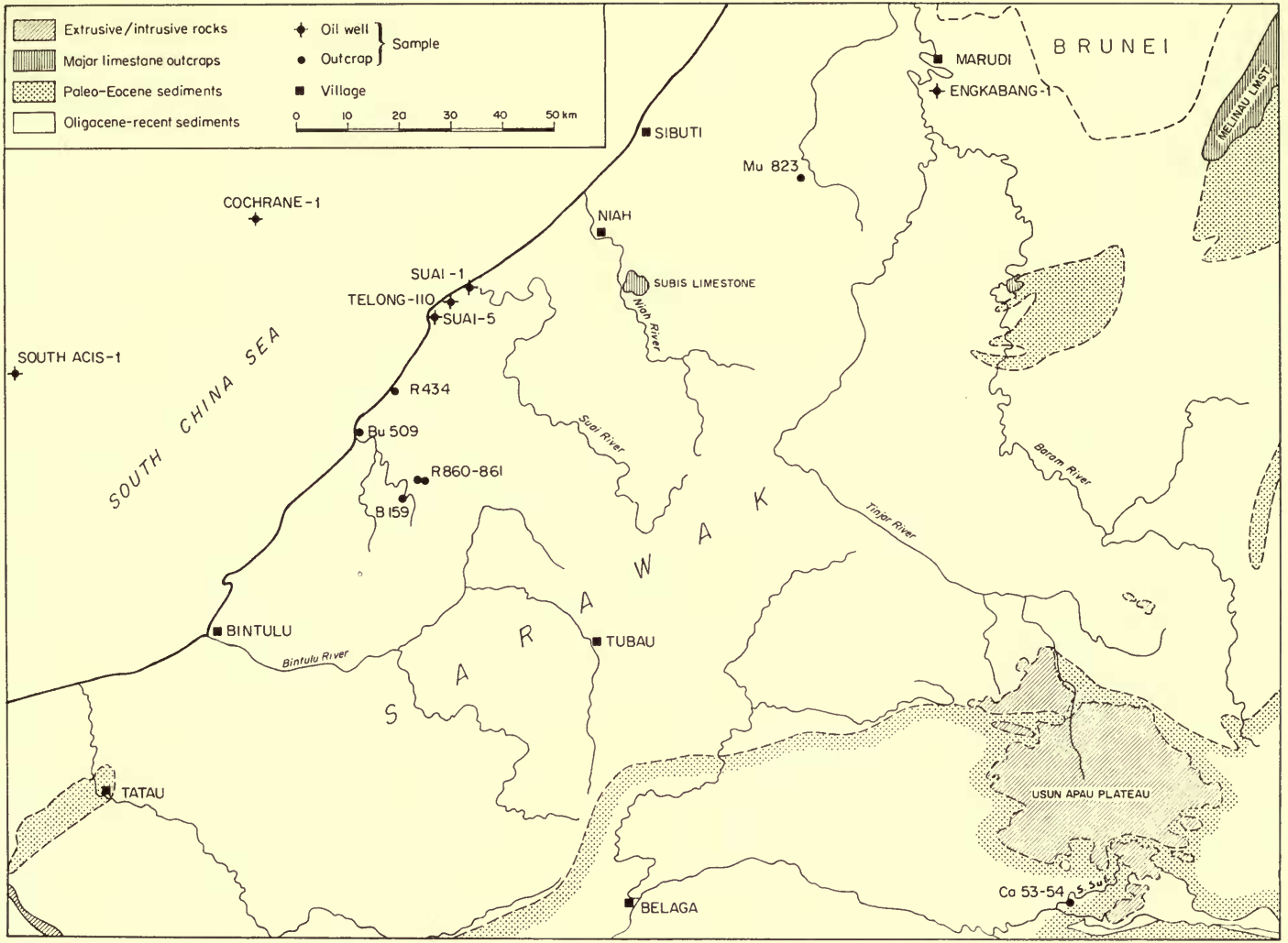


FIG. 2. *Skylonia* localities in Sarawak, Malaysian Borneo.

Republic with *S. dohmi* (Sandberg). *S. sandbergi* ranged up into the Middle Miocene, when it was replaced by *S. thomasi* n. sp., a species known with two subspecies and a few related forms from Borneo, the Philippines, Indonesia, Fiji and Kenya. The youngest representatives of this species probably reached up into the Pliocene (Kenya, Indonesia). During the Middle Miocene the type-species of the genus, *S. mirabilis* Thomas, lived in Kenya. Fragments of specifically unidentified forms were found in the Miocene of Florida (U.S.A.), i.e. *Skylonia* sp. B, and the Upper Miocene of Eastern Indonesia and the Philippines, i.e. *Skylonia* sp. A, and they may well belong to still undescribed species.

TABLE 3

Ranges of *Skylonia* species

	Eocene		Oligocene			Miocene			Pliocene
	M.	Upper	L.	M.	U.	Lower	M.	Upper	
Skylonia bermudezi n. sp.	———								
sarawakensis n. sp.					——				
sandbergi n. sp.						———			
dohmi (Sandberg)						——			
mirabilis Thomas							———		
thomasi n. sp.							———		– ?

V. SYSTEMATIC DESCRIPTIONS

Order CHEILOSTOMATA Busk, 1852

Suborder ANASCA Levinsen, 1909

Family **SKYLONIIDAE** Sandberg, 1963

Genus ***SKYLONIA*** Thomas, 1961

(Synonym, ***FUSICANNA*** Sandberg, 1962)

TYPE SPECIES. *Skylonia mirabilis* Thomas, 1961.

DIAGNOSIS. Skyloniidae with zoarium composed of elongate spindles, tapering symmetrically and with zooecia arranged quadriserially. A single anascaform zooecium at proximal end. Zooecia usually with frontal closure, each with a small, central, usually circular or transversely elongate aperture. No ovicells or avicularia.

REMARKS. *Skylonia*, originally introduced as a problematical fossil, bears only a remote resemblance to other genera of the Cheilostomata Anasca, e.g. *Fusicellaria* d'Orbigny, 1851, or *Encicellaria* Keij, 1969.

RANGE. Middle Eocene to Late Miocene, probably even Pliocene.

DISTRIBUTION. Circumtropical and subtropical.

Skylonia mirabilis Thomas

(Pl. 3, figs. 10–13)

1961 *Skylonia mirabilis* Thomas, 360–363, pl. 13.
1963 *Skylonia mirabilis* Thomas; Sandberg, 4–14, fig. 3—nos. 6 and 7.

Distribution. Middle Miocene of Gaji Hill, west of Malindi and in Ngombeni quarry at Mafia Island, Kenya. According to Dr W. J. Clarke also occurring in sediments of approximately the same age on Zanzibar Island, but no material was available for study.

Diagnosis. *Skylonia* with spindles with twelve to fifteen hexagonal zooecia per longitudinal row, with apertures in the widest part of the spindle only slightly wider than high and situated at the crest of the domal elevation of frontal wall.

Remarks. The spindles, which are 1·4 to 1·7 mm long, 0·29 to 0·36 mm wide (Sandberg, p. 7), are narrow and taper evenly towards both ends, with the proximal end often somewhat curved. The hexagonal shape of the zooecia and the simple domal elevation around the circular to somewhat transversely elongate aperture appear to characterize this species. A tendency was observed towards the development of low knobs flanking the apertures in the widest part of the spindles. In the few spindles in which the proximal end is not broken off it appears that this species has proximal pores in the initial zooecia of the lateral rows (Pl. 3, figs. 11b and 13). One specimen was observed to have a pore above the initial zooecium (Pl. 3, fig. 13). Communication-pores were found by Thomas between adjacent zooecia in the same vertical row, but not between zooecia of adjacent rows. This must be due to the mediocre preservation of the Kenya specimens because they do occur in other species, e.g. *Skylonia dohmi* and *S. thomasi*.

The material is deposited in the British Museum (N.H.) under numbers Z 934–956, 859–894 and in Leiden under RGM 172533–172535.

Skylonia bermudezi n. sp.

(Pl. 2, figs. 1–4)

Name. In honour of Prof. Dr P. J. Bermudez, Caracas, Venezuela.

Type locality. Jabaco at 4½ km west of Guanajay, Province of Pinar del Rio, Cuba (loc. B 337A of Bermudez, 1950, p. 240).

Type stratum. Jabaco Formation of Late Eocene age.

Holotype. Spindle in slide D 51855 (British Museum).

Paratypes. Fourteen spindles from type locality (D 51856–51869) and (RGM 172524), one fragment of a spindle from the same Formation collected at ½ km south of Ingenio Saratoga, Matanzas Province, Cuba (Bermudez loc. B 322) (RGM 172525), and one spindle of Middle Eocene age derived from the Loma Candela Formation at Loma Candela, Province of Pinar del Rio, Cuba (Bermudez loc. B 261, 1950, p. 244).

Diagnosis. *Skylonia* with spindles with seven to ten zooecia per vertical row, apertures with well-developed raised rim and with one to three frontal pores in the terminal zooecia at both ends of spindle.

Description. Spindles are widest near the middle, varying in width between 0·46 and 0·68 mm, and sometimes slightly curved, with seven to ten zooecia per vertical row. The frontal closure is mostly rectangular in outline but in some spindles

the proximal and distal boundaries are arched. The largest zooecia are found near the middle of the spindles, widths varying from 0·32 to 0·41 mm, and lengths varying from 0·15 to 0·19 mm.

The apertures are nearly circular to somewhat transversely elliptical, 0·05 to 0·07 mm in diameter, surrounded by a conspicuous raised rim (Pl. 2, fig. 3) or by a less well-developed rim supplemented by two low knobs flanking the aperture (Pl. 2, fig. 1). These knobs are best developed in the middle part of the spindle.

Frontal pores are present in the first and last two zooecia of each row, there are usually three per zooecium, but occasionally only one or two were observed.

Remarks. In the Middle Eocene Lower Guayabal Formation of the Rio Tecolutla area of Mexico, some badly preserved spindles were found (Pl. 2, fig. 4—RGM 172526–27) which are somewhat differently shaped but very probably belong to *Skylonia bermudezi* n. sp. The number of zooecia per vertical row is slightly lower, i.e. six to nine. No raised rim round the apertures or paired flanking knobs were found, nor raised edges of the frontal plates, because the spindles were worn smooth. More than one frontal pore is present at least at one end of each spindle. This Mexican sample was collected by Mr R. Wright Barker in the upstream area of the Rio Tecolutla from the south bank of the Chumatlan River, a few miles upstream from its confluence with the Rio Espinal, State of Veracruz.

Skylonia dohmi (Sandberg)

(Pl. 2, figs. 5–7)

1962 *Fusicanna dohmi* Sandberg, 65, figs. 12–16.
1963 *Skylonia dohmi* (Sandberg), Sandberg : 1–19, figs. 1–5.

Distribution. Lower Miocene Baitoa Formation of the Dominican Republic and the Middle Miocene Biche limestone Member of the Brasso Formation of Biche quarry, Trinidad (samples DB 268 and WHB 153). Also in unnamed Lower Miocene beds in Union Oil Company of California off-shore boring Martinez-Reef no. 1 at 500, 560 and 640 m depth, off-shore Nicaragua (N 14°34′09″–W 82°32′11″).

Diagnosis. *Skylonia* with spindles with thirteen to fifteen zooecia per longitudinal row, proximal frontal pores in end zooecia of all four rows, the apertures in the middle part of each spindle transversely elliptical and with a conspicuous raised rim.

Remarks. This species was described in detail by Sandberg (1963).

The preservation of the Dominican specimens is excellent, that of those from Trinidad very poor, but they retained enough of their features to allow a specific allocation.

Of the Indo-malaysian species, *S. thomasi* n. sp. resembles *S. dohmi* most closely, but differs in having fewer zooecia per vertical row (only eleven to thirteen) and in having a less well-developed raised rim round the apertures, although some spindles have two low knobs flanking the aperture (Pl. 2, fig. 6). The American species, moreover, has proximal frontal pores in the end zooecia of all four rows, whereas they are restricted to the lateral rows in all the Indo-malaysian species.

The material is deposited in the British Museum under numbers Z 978–984, D 51492–51495 and in Leiden under RGM 172528–532.

Skylonia sandbergi n. sp.

(Pl. 1, figs. 10–13)

NAME. In honour of Dr P. A. Sandberg, Urbana, Illinois, U.S.A.

TYPE LOCALITY. Cochrane well 1, off-shore Sarawak at N 5°54′38″–E 113°07′08″, South China Sea.

TYPE STRATUM. Unnamed formation at 7519 ft depth and of Early Miocene age.

HOLOTYPE. Spindle (D 51709).

PARATYPES. Several spindles and fragments (D 51710–51853 and RGM 172536–540) from the following localities in Sarawak: Suai well 1 (400–1903 ft depth)—Early Tertiary *f* or Early Middle Miocene; Telong corehole 110 (265–274 ft depth)—Late Tertiary *e* or Early Miocene; Cochrane well 1 (4120–7520 ft depth)—Late Tertiary *e* to Early Tertiary *f* or Early to Middle Miocene; Engkabang well 1 (3567–3890 ft depth)—Late Tertiary *e* or Early Miocene; South Acis well 1 (4600–4650 ft depth)—Early to Middle Miocene; outcrop sample J 1065—Early Tertiary *f* or Early Middle Miocene; outcrop sample Mu 823—same as above (see text fig. 2 for locations).

DIAGNOSIS. *Skylonia* with spindles with eight to eleven zooecia per longitudinal row, the zooecia rectangular in outline, apertures circular or higher than wide, frontal pores only in terminal zooecia of lateral rows.

DESCRIPTION. The length and width of the few complete spindles vary from 1·0 mm long by 0·31 mm wide to 1·27 mm long by 0·35 mm wide. The spindles reach their maximum diameter at or just below the middle. Each longitudinal row consists of eight to eleven zooecia of a rectangular shape. The width of the zooecia varies between 0·29 and 0·38 mm, but most are between 0·32 and 0·34 mm wide. The width/length ratio of the median zooecia varies between 1·3 and 2·1 mm. Only the terminal zooecia of the lateral rows carry proximal frontal pores. The apertures are circular or somewhat higher than wide. In some well-preserved specimens the proximal side of the aperture is slightly sinuous (Pl. 1, figs. 11a and 12). The apertures are situated in the centre of a generally low elevation. The width of the aperture of the median zooecia varies from 0·04 to 0·07 mm. The apertures above the spindle's greatest diameter open obliquely upwards. The distal end of the frontal cover is depressed, forming a shallow groove. Only rarely two low, lateral knobs flank the aperture.

Each zooecium is connected with each of the surrounding ones by means of a minute communication-pore.

REMARKS. *Skylonia sandbergi* n. sp. differs from *S. mirabilis* Thomas in the shape of the zooecia, which are rectangular and not hexagonal, and in the shape of the aperture. *S. sandbergi* differs from *S. dohmi* (Sandberg) and *S. thomasi* n. sp. in the absence of a well-developed elliptical raised rim round the apertures, and of

well-developed knobs flanking the aperture and in the smaller number of zooecia in each longitudinal row.

Skylonia sarawakensis n. sp.

(Pl. 3, figs. 1–7)

NAME. After the State of Sarawak, Malaysian Borneo.

TYPE LOCALITY. Tanjong (Cape) Semilajau (sample Bu 509), Sarawak.

TYPE STRATUM. Nyalau Formation of Early Miocene age (*Globorotalia kugleri* zone).

HOLOTYPE. Spindle (D 51501).

PARATYPES. One hundred and seventy specimens (D 51502–51664 and RGM 172541–172544) all collected from the Nyalau Formation at Sungei (River) Sut

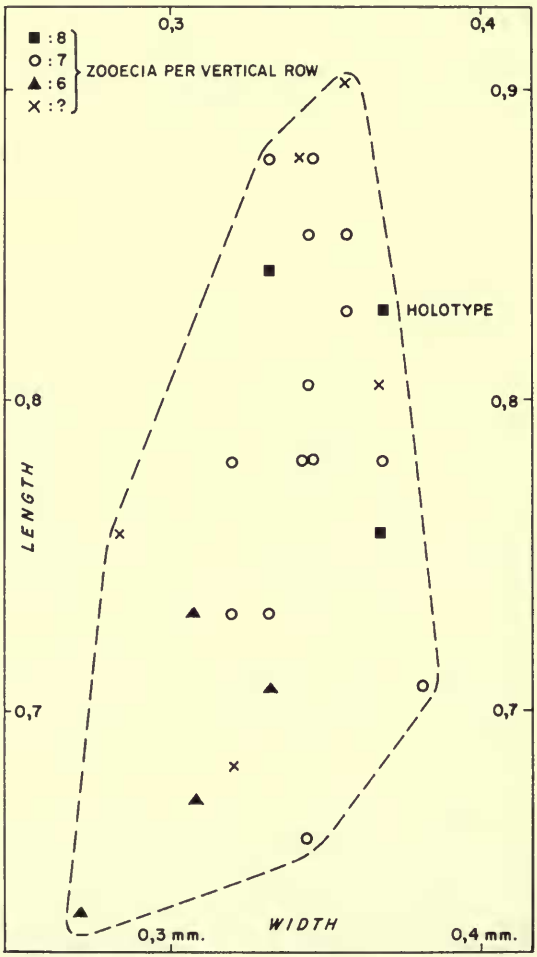


FIG. 3. Length and width measurements on *Skylonia sarawakensis* n. sp.

(samples Ca 53 and 54), Sungei Selungun (sample R 434), Sungei Perihas (samples R 860 and 861) and Sungei Sigrok (sample B 159) and Suai well 5 (4790–4800 ft depth), Sarawak (see text fig. 2).

DIAGNOSIS. *Skylonia* with spindles rather thick-set, with six to eight zooecia in each longitudinal row and with apertures of zooecia on the widest part of the spindle with two conspicuous and smooth flanking knobs.

DESCRIPTION. The shape of the spindles is variable, the maximum width is at the middle or above it. A number of spindles were measured and the result plotted in text fig. 3. Most of the spindles are slightly damaged or worn at their ends and the measured length is always slightly less than the original one.

Each longitudinal row consists of six to eight zooecia. The terminal zooecia are higher than wide, the others much wider than high. Their shape is rectangular or hexagonal, the proximal and distal boundaries being long and straight, the lateral ones straight or slightly zig-zag. The maximum width of the zooecium is 0·22 mm and the maximum height 0·13 mm.

The shape of the aperture changes from higher than wide (0·07 mm) at the proximal end, through circular to horizontal and slit-like (0·03 to 0·06 mm wide) in the middle of the spindle and back to somewhat higher than wide at the distal end.

A well-developed and thick rim is present round the apertures of all zooecia except that of the initial one. Three or four zooecia near the middle of the spindle have two large, smooth knobs flanking the slit-like aperture. The two preceding and the two succeeding zooecia feature only weakly developed knobs.

Frontal pores are present in this species (Pl. 3, fig. 2), but due to the bad preservation, only one good example was found in a proximal zooecium of a lateral row. In several specimens no such pore was observed in the frontal row.

Skylonia thomasi n. sp.

NAME. In honour of the late Dr H. D. Thomas.

DIAGNOSIS. *Skylonia* with spindles with more than ten zooecia in each longitudinal row, the apertures transversely elongate and with a low raised rim or two flanking knobs, proximal and distal zooecial boundaries slightly curved towards the distal end and with proximal frontal pores in the terminal zooecia of the lateral rows only.

REMARKS. Two forms were found, one in sediments of Late Tertiary *f* age or Middle Miocene, on Madura (Indonesia), the other in sediments of Tertiary *g* or Late Miocene age in Sabah (Malaysian Borneo). They are treated here as two subspecies as they differ only in subordinate characters.

Three fragments of a stout form were collected from Uppermost Miocene or Lowermost Pliocene (i.e. *Globorotalia margaritae* zone) beds in well Lamu-2 (596–600 ft depth) in Kenya (RGM 172545). In the shape of the frontal plate and the raised rim these fragments show affinity with *Skylonia thomasi* n. sp., but complete spindles are needed for a full evaluation. The maximum width of these fragments varies

between 0·44 and 0·46 mm, the maximum width of the zooecium is 0·29 mm and its height 0·15 mm. The maximum width of the aperture is 0·07 to 0·09 mm.

Another fragment with wide open zooecia (Pl. 4, fig. 7) was found in a sample from the Thuvu sediment Group of Late Miocene age (*Globorotalia margaritae* zone, lower part) at the southeast coast of Vitu Levu, Fiji Islands (RGM 172546). Here again an affinity with *Skylonia thomasi* n. sp. is assumed. *S. thomasi* somewhat resembles *S. dohmi* (Sandberg) in the outline of the spindle and in the configuration of the raised rim. It differs in having frontal pores in the lateral rows only and not in all four rows as in *S. dohmi*, which lacks the flanking knobs of the apertures and has a slightly higher number of zooecia per vertical row.

Skylonia thomasi thomasi n. sp. *et* n. subsp.

(Pl. 4, figs. 1–4)

Type locality. Outcrop at N 5°13′–E 119°04′07″ (sample Jo 121), Dent Peninsula, Sabah, Malaysian Borneo.

Type stratum. Sebahat Formation of Late Miocene age (Tertiary *g*).

Holotype. Spindle D 51665.

Paratypes. Thirty-four spindles or fragments (D 51666–51698 and RGM 172547).

Distribution. Only in the Sebahat Formation at the type locality and at N 5°13′03″–E 119°04′02″ (sample Mt 2196).

Diagnosis. *Skylonia thomasi* with spindles widest below the middle, with eleven to thirteen zooecia in each longitudinal row and a straight proximal end with the initial zooecium in the same plane as the succeeding zooecia of the frontal row.

Description. The spindles are approximately 1·5 mm long and 0·37 mm wide with their maximum width below the middle.

The initial zooecium has a relatively large aperture of 0·07 mm high and 0·04 mm wide, which is surrounded by a low rim. The shape of the apertures changes from circular to transversely elongate (0·04 mm wide) in the middle part of the spindles. The raised rim is either low and rounded or developed as two small smooth knobs flanking the apertures (Pl. 4, fig. 4). A groove de-limits the elliptical outer edge of the raised rim.

The shape of the zooecia changes from higher than wide at both ends to much wider than high (0·23 to 0·24 mm wide by 0·11 mm high) in the middle part of the spindle. The proximal and distal margins of the zooecia are somewhat curved.

In the very few complete spindles available, it was observed that the longitudinal rows contain eleven to thirteen zooecia. Only the proximal and distal zooecia of the lateral rows show a small circular frontal pore at their proximal end.

Each zooecium is connected with the surrounding six zooecia by a minute communication-pore (Pl. 4, fig. 2).

REMARKS. This subspecies differs from the slightly older subspecies *Skylonia thomasi madurensis* n. subsp. in the shape of the spindles and in the shape of the proximal end.

Skylonia thomasi madurensis n. sp. *et* n. subsp.

(Pl. 4, figs. 5–7)

NAME. After the Island of Madura, Indonesia.

TYPE LOCALITY. Kali (river) Ambunten (sample Be 1421), approx. 3 km SSE of Ambunten village, East Madura.

TYPE STRATUM. Sediments of Tertiary f_3 age or Middle Miocene.

HOLOTYPE. Spindle D 51699.

PARATYPES. Four spindles and one fragment (D 51700–51705).

DISTRIBUTION. A single specimen from ditch-cuttings of Cochrane well 1 (4140–4150 ft depth), off-shore Sarawak and of supposedly Middle Miocene age, very probably also belongs to this subspecies.

DIAGNOSIS. *Skylonia thomasi* with spindles long and narrow with sides nearly parallel, the proximal end curved forward, the initial zooecium making an angle with the succeeding zooecia of the frontal row.

DESCRIPTION. The spindles are long (more than 1·5 mm) and narrow with the proximal end curved forward, causing the initial zooecium to make an angle of approximately 45° with the axis of the spindle. Their maximum width is 0·37 mm.

The number of zooecia per vertical row is unknown but is definitely more than eleven. The maximum width of the zooecia in the median part of the spindle is 0·23 mm and their height 0·13 mm. In the terminal zooecia a raised rim is present round the apertures. In the middle part of the spindles it is well developed and elliptical in shape, often with two smooth knobs flanking the apertures. The distal end of the raised rim merges in a depression which is probably ornamented with a number of low vertical ridges. The shape of the aperture is difficult to determine with certainty due to the mediocre preservation of the material, but the usual change from vertically elongate through circular to transversely elongate was observed. The outline of the zooecia is rectangular with slightly curved proximal and distal boundaries.

Proximal frontal pores were observed in the end zooecia of the lateral rows only.

Skylonia sp. A

(Pl. 3, fig. 8)

REMARKS. Two fragments of a species with rectangular unornamented zooecia were found in the Klasaman Formation at Waileh on Salawati Island, opposite the west end of Bird's Head Peninsula, New Guinea. The age is Late Miocene or Pliocene. One fragment is badly corroded, the other is smaller and well preserved.

It shows that the zooecia are rectangular and slightly convex and the central openings are transversely rectangular. These fragments probably belong to a new species but more material is needed to define it properly.

Three very badly preserved fragments, probably belonging to the same species, occurred in a sample of the Berili Marl, at approx. 4 km ESE of Aloguinsan on Cebu Island, Philippines. Their age is Late Miocene.

The material is stored under numbers D 51496–51500.

Skylonia sp. B

(Pl. 3, fig. 9)

Remarks. A single fragment of a rather well-preserved specimen from the Lower Miocene Chipola Formation at Fairley Creek in Florida (sample T.U. 823), and a heavily decalcified fragment from the same formation at Chipola River (sample T.U. 548) was obtained for study through the courtesy of Dr R. J. Scolaro. The well-preserved fragment is 0·73 mm long and comprises three or four zooecia per vertical row. The proximal end is broken off, but two of the zooecia of opposite rows are apparently the first lateral zooecia as two frontal pores are present. The fragment belonged to a still functional spindle, as the opesiae have not been covered yet by the calcified frontal plates with their small central openings. The openings change in shape from vertically elongate (0·06 to 0·07 mm wide and 0·10 mm high) to circular with a diameter of 0·10 mm. The fragment T.U. 548 shows that the openings ultimately become small and nearly circular.

VI. REFERENCES

Bermudez, P. J. 1950. Contribucion al estudio del Cenozoico cubano. *Mem. Soc. Cub. Hist. Nat. "Felipe Poey"*, Habana, **19** : 3, 205–375.

Canu, F. & Bassler, R. S. 1920. North American Early Tertiary Bryozoa. *Bull. U.S. nat. Mus.*, Washington, **106** : 1–879, 162 pls.

Labracherie, M. 1968. Quelques bryozoaires cheilostomes de la Falaise de Handia (Biarritz, France). *Atti Soc. Ital. Sci. Nat. Museo Civ. Stor. Nat. Milano*, **108** : 312–326, pls. 7–10.

Liechti, P., Roe, F. W. & Haile, N. S. 1960. The geology of Sarawak, Brunei and the western part of North Borneo. *Bull. Geol. Surv. Brit. Terr. Borneo*, Kuching, **3** (2 vols.).

d'Orbigny, A. 1851. *Paléontologie Française. Terrains Crétacés.* V. *Bryozoaires*, pp. 1–188.

Reuss, A. E. 1848. Die fossilen Polyparien des Wiener Tertiärbeckens. *Haidinger's naturwiss. Abh.* II (1847) : 1–109.

Sandberg, P. A. 1962. New cheilostome Bryozoa from the Miocene of the Dominican Republic. *Micropal.*, New York, **8** : 61–66.

—— 1963. The affinities of *Skylonia* to the cheilostome Bryozoa. *Stockholm Contr. Geol.*, **11** : 1–19.

Stach, L. W. 1936. Correlation of zoarial form with habitat. *Journ. Geol.*, Chicago, **44** : 1, 60–65.

Thomas, H. D. 1961. *Skylonia mirabilis* gen. et sp. nov., a problematical fossil from the Miocene of Kenya. *Ann. Mag. Nat. Hist.*, London, ser. **13**, **4** : 359–363, pl. 13.

This paper was intended to precede a second contribution by the author, dealing with related Eocene and Oligocene skyloniid genera, but owing to unforeseen delays the order of publication was reversed. The reader is referred to KEIJ, A. J. 1972. *Sylonika* and *Kylonisa*, two new Palaeogene bryozoan genera (Cheilostomata, Skyloniidae). *Scripta Geol.* **11**: 1–15.

A. J. KEIJ
c/o SHELL INTERNATIONALE PETROLEUM
MAATSCHAPPIJ B.V.
POSTBUS 162
THE HAGUE
NETHERLANDS

PLATE 1

Planicellaria fenestrata d'Orbigny

FIG. 1. Part of internode with three occluded zooecia. Lower Thanetian of Musitu, Spain. ×18.

Vincularia fragilis (Defrance)

FIG. 2. Two zooecia with abnormally deep-lying calcareous closures; normal, flush closures usually show opercular scars. Lower Lutetian of Nalinnes, Belgium. ×35.

Stamenocella oculata (Ulrich & Bassler)

FIG. 3. Proximal end of internode with large initial zooecium which remained uncalcified in contrast to the succeeding zooecia which have nearly complete frontal closures. Note presence of opercular scars. Paleocene Vincentown Marl at Rancocas Creek, Burlington County, New Jersey, U.S.A. ×18.

" Smittipora " sp.

FIG. 4. Proximal end with small calcified initial zooecium with minute central pore. Ypresian of marlpit of Sourbet, Horsarrieu near St Sever (Landes), France. ×18.

" Cellaria " mucronata Meunier & Pergens

FIG. 5. Proximal end with large anascaform initial zooecium completely open. Montian Calcaire de Mons in boring Obourg (depth 56 m) near Mons, Belgium. ×18.

Vibracella (Discovibracella) oculata Voigt

FIG. 6. Few of the zooecia are calcified, leaving a slit-like opening. Opercular scars present. Montian Calcaire de Mons in boring Obourg (depth 56 m) near Mons, Belgium. ×18.

Nellia tenuis Harmer

FIG. 7. Proximal end with calcified initial zooecium. Recent, South China Sea at N 5°59′–E 112°35′ at 430 m depth. ×35.

Scrupocellaria milneri Canu & Bassler

FIG. 8. Two of the figured zooecia are calcified, the third one not. Oligocene Byram Marl of type locality at Byram station, 7 miles north of Jackson, Mississippi, U.S.A. ×35.

Encicellaria hofkeri Keij

FIG. 9. Incomplete spindle with initial zooecium and two succeeding zooecia occluded and remainder of zooecia open. Maastrichtian Maastricht Limestone in ENCI quarry near Maastricht, Netherlands. ×18.

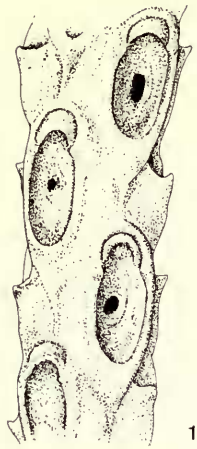
Skylonia sandbergi n. sp.

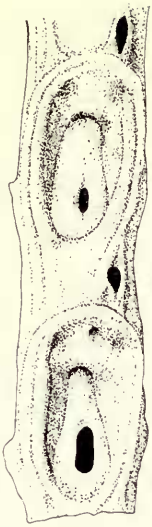
FIG. 10. Middle part of spindle. Lower Miocene, Engkabang well 1 (3580–3590 ft depth), Sarawak. ×35.

FIG. 11. (a) Complete spindle from the side and (b) proximal end seen from the front with its large initial zooecium. Lower Miocene of Cochrane well 1 (7510–7520 ft depth), off-shore Sarawak in South China Sea. Holotype. ×35.

FIG. 12. Part of spindle. Same well and age at 5370–5380 ft depth. ×35.

FIG. 13. Distal half of spindle with the zooecia not closed with calcified lamellae. Lower Miocene of Suai well 1 (core of 1897–1903 ft depth), Sarawak. ×35.

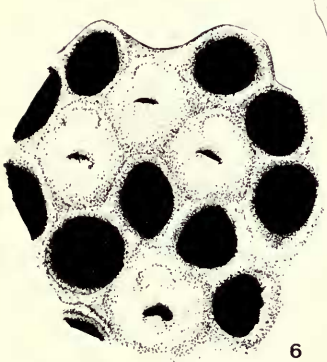

1


2

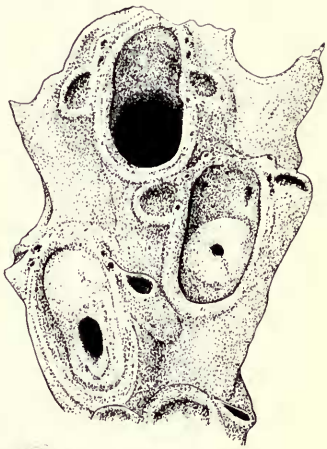

3


4

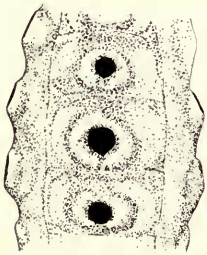

5

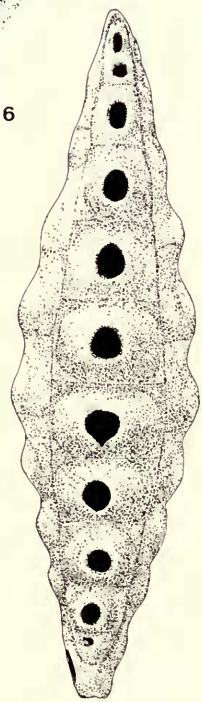

6


7

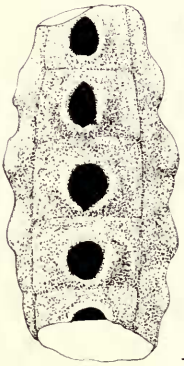

8


9


10


11a


11b


12

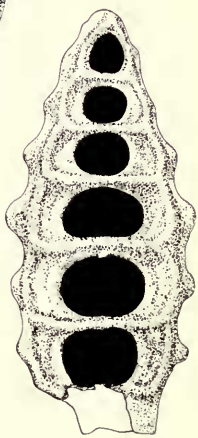

13

PLATE 2

Skylonia bermudezi n. sp.

FIG. 1. Nearly complete spindle with calcified zooecia and three frontal pores in the proximal and distal zooecia. ×35.

FIG. 2. Spindle with the frontal closure not yet at full extension. ×35.

FIG. 3. Large, incomplete spindle with frontal closures and small central openings (Holotype). ×35.

Upper Eocene Jabaco Formation of Jabaco (loc. Bermudez B 337A), Cuba.

FIG. 4. Badly preserved spindle which probably belongs to this species. Middle Eocene Lower Guayabal Formation of Chumatlan River, Mexico. ×35.

Skylonia dohmi (Sandberg)

FIGS. 5–7. 5. Distal end of spindle showing presence of single frontal pores in distal zooecia.

6. Middle part of spindle with low knob-like protrusions flanking the slit-like central openings.

7. Proximal end of spindle from the side showing presence of single frontal pores in proximal zooecia.

Lower Miocene Baitoa Formation of Dominican Republic. ×35.

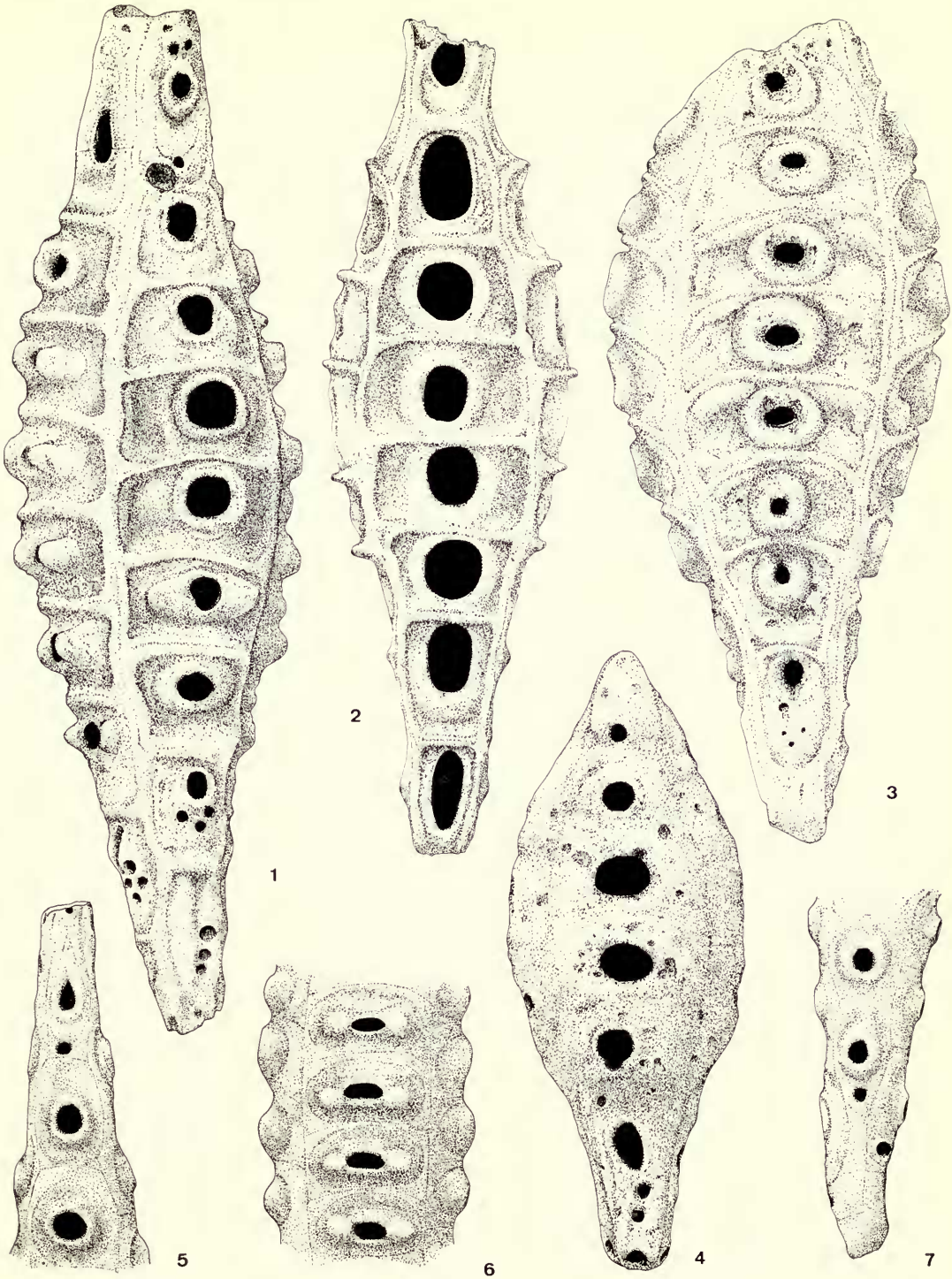

1
2
3
4
5
6
7

PLATE 4

Skylonia thomasi thomasi n. sp. *et* n. subsp.

FIG. 1. (a) Complete spindle from the side, (b) proximal end of spindle, (c) proximal part of spindle with initial zooecium, (d) distal end of spindle. Holotype.

FIG. 2. Distal end of fragment of spindle showing pores between zooecia in all four rows.

FIG. 3. Fragment of spindle without frontal closures.

FIG. 4. Middle part of spindle in which low knobs flank the elliptical central opening.

Upper Miocene Sebahat Formation, Dent Peninsula, Sabah. ×35.

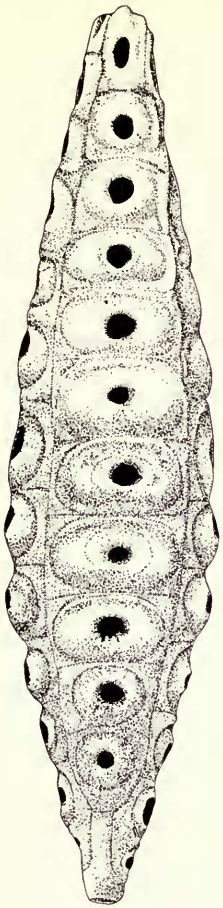
Skylonia thomasi madurensis n. sp. *et* n. subsp.

FIG. 5. (a) Nearly complete spindle from the side, (b) proximal end, (c) proximal part with initial zooecium, (d) proximal part from the side. Holotype.

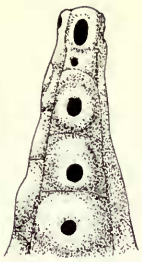
FIG. 6. Proximal end of spindle lacking frontal closures of the zooecia.

Middle Miocene of Kali Ambunten, Eastern Madura, Indonesia. ×35.

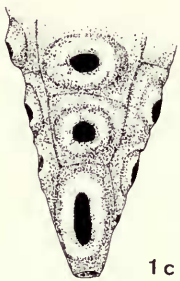
FIG. 7. Fragment of spindle found in Upper Miocene Thuvu Group of Viti Levu, Fiji Islands. ×35.



1a



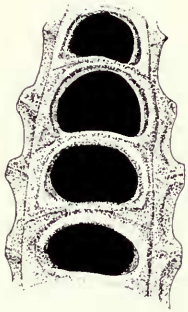
1d



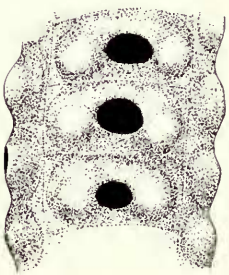
1c

1b

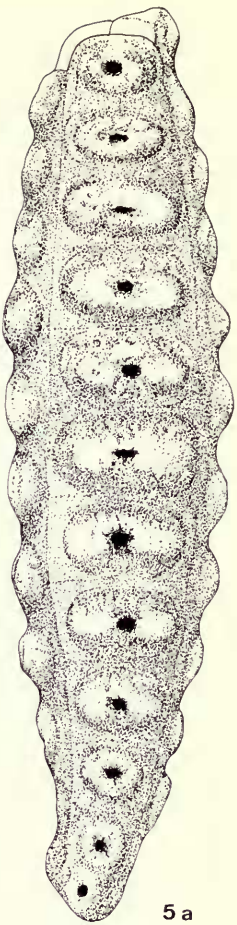
2



3

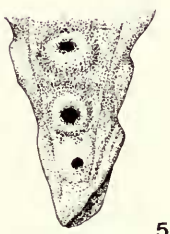


4

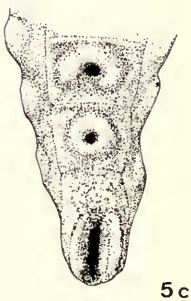


5a

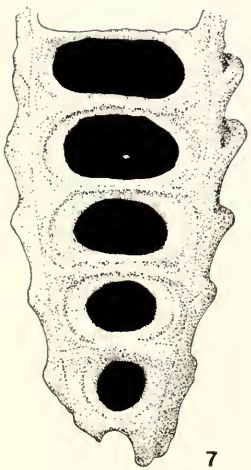
5b



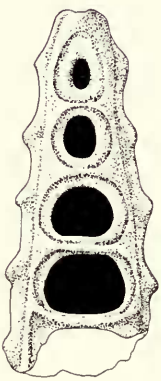
5d



5c



7



6